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FOSSIL LIZARDS FROM THE DOMINICAN REPUBLIC

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THE known history of West Indian lizard faunas does not extend very far into the past. The remains of lizards have been recovered from Indian middens and from cave deposits on a number of islands, but even the oldest cave fossils are probably not older than late Pleistocene. Nevertheless, these remains clearly indicate that the island lizard faunas of the not-too-distant past were markedly different from those on the islands today. They include species that are now extinct, some of which were larger than any living member of their genus. They also include living species that occur on the same island today but which attained a greater maximum size, and living species that are now found only on other islands (Hecht, 1951; Etheridge, 1964 and unpublished data).

The pattern of late Pleistocene extinction and gigantism found in West Indian lizards is similar to that found in the island mammals and the mammals of the North American continent, but quite unlike the Pleistocene history of the continental lizard faunas. Of the many lizard species reported from the Pleistocene of Florida (Auffenberg, 1955, 1956; Holman, 1958, 1959a, 1959b, 1962a; Gut and Ray, 1963), of Oklahoma (Etheridge, 1960a), of Texas (Holman, 1962b, 1963), of Kansas (Etheridge, 1958, 1960b, 1961), and of California (Brattstrom, 1953, 1954, 1955, 1958) none of them is now extinct and only one of them grew to a larger or smaller maximum size than it does today. Undoubtedly the changing climate of the Pleistocene greatly influenced the distribution of lizards on the continent, for some forms are known to have lived beyond their present range. Otherwise, at least insofar as their fossils indicate, North American lizards do not seem to have been much influenced by Pleistocene events.

The present study of lizard remains from a cave in the western part of the Dominican Republic contributes additional evidence that the lizard faunas of the West Indies, unlike those of the North American continent, have undergone dramatic changes in the not remote past.

CERRO DE SAN FRANCISCO CAVE

On August 7, 1958, Dr. Clayton E. Ray and his field party from the Museum of Comparative Zoology at Harvard excavated an exceedingly rich fossil deposit in a cave in the western part of the Dominican Republic. The cave lies in the top of Cerro de San Francisco, an isolated hill directly east of Fortaleza Pedro Santana in the province of San Rafael, adjacent to the Haitian border. Cerro de San Francisco is indicated on the United States world aeronautical chart above the 2000 foot mark at latitude $19^{\circ} 6' N$, longitude $71^{\circ} 41' W$.

According to Ray's field notes (Aug. 7-8, Aug. 31-Sept. 2, 1958) Cerro de San Francisco is an isolated limestone block. The cave, standing as it does high in this isolated hill, has no part in the present drainage of the land, but is clearly part of an older drainage system. The cave is quite large, with at least three large skylights. Its floor is very dry and has many large and small pieces of roof debris. A pit was dug near the rear wall of the cave and another about 10 feet out toward the middle of the cave, both to a depth of about seven feet. The pit near the wall descended through well marked strata containing many fossils, the one nearer the middle of the cave descended through powdery white guano containing no bone. On the basis of the pit near the rear wall Ray divided the floor material into three bone-bearing strata as follows:

Stratum 1. Surface to about 15 inches in depth, consisting of two subdivisions as follows:

A. Upper unit, 12 inches thick. A brown earth with much goat dung and bone near its surface. Most of the bones were owl pellet components and were mainly of *Rattus*.

B. Lower unit, 4-6 inches thick. A light gray, fluffy, ashy deposit, very light weight and powdery, containing almost no bone.

Stratum 2. Six to 12 inches thick. A dark brown earth with irregularly distributed black lenses. At least one of the lenses contained a potsherd and several charred sticks, and appeared to be a cook fire. The bones were distributed through the brown and black portions of the stratum but occurred primarily in a band about one foot thick and one foot below the surface. The stratum seems to be an owl deposit judging from its composition: *Nesophontes*, bats, birds, lizards, frogs, and a few very young individuals of *Isolobodon* and *Brotomys*. The stratum also contained human bone fragments.

Stratum 3. Three to 4 feet in thickness. A yellowish brown earth extending from a sharp border with the darker earth of *Stratum* 2 to a lower stratum of limestone rubble. The stratum contained *Isolobodon*, *Brotomys*, *Plagiodontia*, *Nesophontes*, sloth, bats, lizards, and birds.

Below *Stratum* 3 is a layer about 1-1½ feet thick of limestone rubble forming a solid floor in places. Below this a layer of very hard, brown earth, possibly an indurated guano, extends for a depth of at least one foot. Neither of these two lower strata contained bone.

The lizard fossils reported here are from *Strata* 2 and 3. Lying as they do below the *Rattus* level, they are almost certainly pre-Columbian in age. The presence of human bone fragments in *Stratum* 2 suggest a maximum age of not more than 4000 years, for according to Rouse (1964) man did not arrive in the Greater Antilles before 2000 B.C. *Stratum* 3 may be much older, but is probably not older than late Pleistocene. The lizard faunas of the two strata are identical in species composition. In spite of their relative youth these cave deposits contain the remains of an extinct snail (Clench, 1962) and a number of extinct vertebrates. Among the lizard fossils is an extinct species of *Leiocephalus* and living forms of *Aristelliger*, *Anolis*, *Leiocephalus*, *Ameiva*, and *Diploglossus*.

In the following account the minimum and maximum snout-vent lengths of the animals from which the fossils came were calculated by multiplying various measurements of the fossils by the ratio of measurements of the same elements of skeletons of modern specimens to their snout-vent lengths. Series of modern skeletons were used to diminish the error introduced by individual variation and ontogenetic changes in proportions.

The type of the extinct *Leiocephalus* is in the Museum of Comparative Zoology at Harvard. All other specimens referred to are in the vertebrate paleontology collections of the Florida State Museum.

GEKKONIDAE

Aristelliger lar Cope 1861

Several hundred fossils of a large gecko are referred to the modern Hispaniolan species *Aristelliger lar*. The criteria used for their generic identification are those given by Hecht (1951) and

Etheridge (1964). Most of existing structural and proportional differences among the species of *Aristelliger* appear to be due only to differences in size. The size disparity is great; maximum snout-vent lengths recorded for each species are: *cochranae* 60 mm, *praesignis* 85 mm, *georgeensis* 115 mm, *lar* 135 mm and *titan* 150 mm (Hecht, 1951).

The maximum size reached in this population was approximately that attained by *Aristelliger lar* today. Calculations of snout-vent lengths from measurements of the smallest and largest fossils of each element are: based on dentaries 66-120, on maxillae 57-121, on parietals 89-117, on quadrates 98-120, on frontals 69-140, on basale 94-120, and on pelves 80-117 mm. Fusion of the parietals, an indication that near-adult size has been reached, does not occur in fossils below calculated snout-vent length of 110 mm. This precludes the possibility that a smaller species is represented by some of the smaller fossils.

The fossils exhibit an ontogenetic increase in the number of teeth on the dentary and maxilla (Fig. 1) similar to that demonstrated in other geckos, *Thecadactylus rapicaudus* (Etheridge, 1964) *Tarentola annularis* and *T. ephippiata* (Grandison, 1961). Tooth counts of modern adult *Aristelliger lar* approximate those of fossils of the same size. Tooth counts of a few individuals of *A. praesignis*, *A. cochranae*, *A. georgeensis*, and *A. titan*, plotted on the same chart, indicate the possibility that *A. titan* may follow the same ontogenetic gradient as *A. lar*, and that the other forms may not. If this proves to be the case then there would appear to be no anatomical reason for considering the extinct Jamaican *A. titan* other than a population of *A. lar* grown to larger size, for they differ only in maximum size attained and number of teeth present at maximum size.

Fossils of *Aristelliger lar* have also been reported from Deep Cave, near St. Michel de l'Atalaye, Department de l'Artibonite, Haiti (Hecht, 1951). This locality and the cave at Cerro de San Francisco lie far outside the range of the species as reported by Cochran (1941): the southwestern peninsula of Haiti and the Samana Peninsula of northeastern Dominican Republic. Hecht suggests that the modern distribution of *A. lar* is probably relict, and the occurrence of fossils outside the present range indicates that at an earlier time the species occupied a wider range on the island than it does today. Dr. Albert Schwartz (*in litt.*) has found the

species at a number of other localities and believes that it occurs rather generally over the entire island. Dr. Schwartz believes that its apparent relict distribution is merely an artifact of collecting, and its rarity in collections is probably due to its strictly nocturnal habits and its preference for large *Ficus* and other trees that have prop roots and are covered with woody vines.

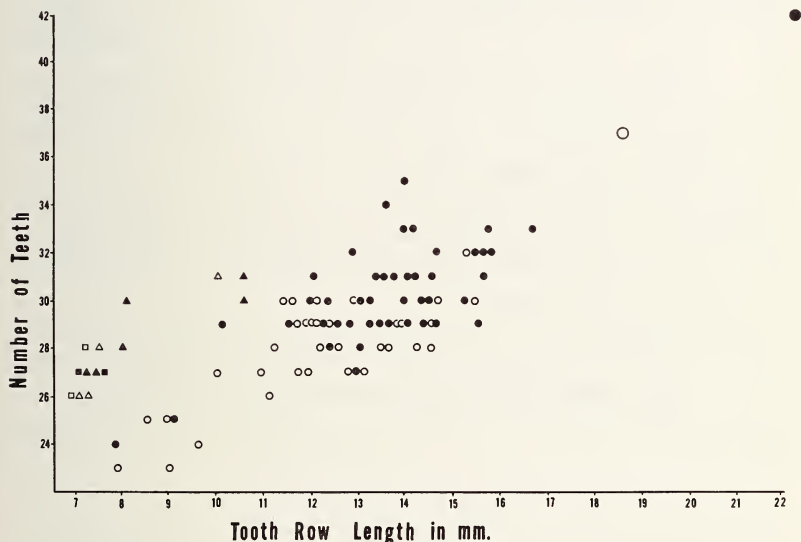


Fig. 1. Ontogenetic increase in the number of teeth on the dentary (solid symbols) and maxilla (open symbols) in *Aristelliger*. Small circles, *A. lar* from Cerro de San Francisco. Large circles, *A. titan*. Triangles, *A. praesignis*, Squares, *A. cochranæ expectatus*. Hexagons, *A. georgeensis*.

Referred Specimens. Dentaries 10051 (141), maxillae 10052 (178), frontals 10053 (66), basale 10054 (9), parietals 10055 (13), quadrates 10056 (10), surangular-articular 10057 (21), pterygoids 10058 (12), pelves 10059 (28), vertebrae 10060 (26).

IGUANIDAE

Anolis ricordii (Duméril and Bibron) 1837

About 80 cranial elements and eight pelves are identical in all major features with modern skeletons of *Anolis ricordii*. They may be distinguished from all other Hispaniolan anoles by their

large size and by the presence of strong rugosities on the upper surfaces of the skull roofing bones.

The fossil population is calculated to have attained a maximum snout-vent length of about 190 mm, larger than that of any living species of *Anolis*. Measurements of the smallest and largest fossils of each element yield the following estimates of snout-vent length: based on dentaries 78-166, on maxillae 155-190, on frontals 112-192, on parietals 84-141, on basale 132-167 mm. Williams (1960) gives the snout-vent length of adult males of *A. ricordii* as about 137 mm. He has informed me (*in litt.*) that the largest specimen in the Museum of Comparative Zoology has a snout-vent length of 159 mm. Thus the species has decreased about 30 mm in maximum snout-vent length.

Fossils of *Anolis ricordii* are also known from Deep Cave near St. Michel de l'Atalaye, Department L'Artibonite, Haiti (Hecht, 1951). *Anolis ricordii* occurs over most of the island and probably in the vicinity of the cave today.

Referred Specimens. Dentaries 10061 (15), maxillae 10062 (41), frontals 10063 (12), parietals 10064 (7), prefrontal 10065 (1), jugals 10066 (3), pterygoids 10067 (2), postorbital 10068 (1), articular-surangulars 10069 (3), basale 10070 (4), quadrate 10071 (1), pelves 10072 (8).

Anolis cybotes Cope 1862

The most abundant lizard remains are those of a moderate-size anole, represented by over 1000 fossils. The dentaries show a distinctive type of sculpturing characteristic of the modern Hispaniolan species *A. cybotes*, *A. armouri*, *A. shrevei*, and *A. whitemani*. At about 40-45 mm snout-vent length, a number of closely spaced, shallow grooves appear on the ventrolateral face of the dentary. The grooves extend from the level of the last few teeth to the level of the dorsal process of the coronoid. Posteriorly the grooves are deepest and all of them end abruptly at the same level; anteriorly they fade out gradually. As the jaw increases in size the grooves deepen and become more irregular. They extend their coverage ventrally and anteriorly, but not posteriorly. With continued growth the ventrolateral face of the element becomes greatly swollen and the irregular grooves are thrown into a series of horizontal, more or less semilunar folds. At maximum size the sculpturing covers all of the ventral and ventrolateral face of the

dentary anterior to the level of the coronoid. Posteriorly the swollen area ends abruptly with a heavily sculptured projection that has a deep recess in its posterior surface. This sequence of ontogenetic changes in the dentary occurs in all of the above mentioned species and, when they are lined up from smallest to largest, in an identical fashion in the fossils. The sculpturings that occur on the lower jaws of other species of *Anolis* (*crisatellus*, *scriptus*, *gundlachi*, *pulchellus*, *krugi*, and *bimaculatus*) have entirely different configurations.

I am unable to distinguish the skeletons of *A. cybotes*, *A. armouri*, *A. shrevei*, and *A. whitemani*. *Anolis cybotes* occurs over most of the island today and in the immediate vicinity of the cave. The other species have more restricted ranges, none of which includes the Cerro de San Francisco. For this reason, and no other, I have tentatively referred the fossils to *Anolis cybotes*.

The fossil population is estimated to have reached a maximum snout-vent length of about 75 mm, slightly larger than that attained by most living populations. Snout-vent lengths calculated for the smallest and largest fossils of each element are: based on dentaries 42-75, on parietals 55-75, on quadrates 58-71, and on basale 58-69 mm. Williams (1960) gives the snout-vent length of adult males of *A. cybotes* as 67 mm. He has informed me (*in litt.*) that the race *A. cybotes haetianus* from the southwestern peninsula of Haiti reaches a maximum of 79 mm, but that over the rest of the island the maximum snout-vent length attained is 70 mm (measurements based on specimens in the Museum of Comparative Zoology).

Referred Specimens. Dentaries 10073 (377), maxillae 10074 (506), postorbitals 10075 (6), frontals 10076 (82), parietals 10077 (28), pterygoids 10078 (2), quadrates 10079 (6), premaxillae 10080 (2), prefrontals 10081 (2), articular-surangulars 10082 (32), jugals 10083 (11), basale 10084 (39), interclavicle 10085 (1), pelves 10086 (44).

Anolis chlorocyanus Duméril and Bibron 1837

A single dentary is referred to *Anolis chlorocyanus*, primarily on the basis of its slender form. The jaw measures 9.4 mm from the symphysis to the posterior border of the last tooth, 1.3 mm deep at the position of the last tooth and 0.9 mm deep midway between the symphysis and the last tooth. Using these three

measurements the fossil has been compared with dentaries of other Hispaniolan anoles by discriminant function analysis programmed for a 1620 IBM computer (Rao, 1958, p. 239). The species number of dentaries compared with the fossil are *A. coelestinus* 3, *distichus* 4, *cybotes* 8, *aliniger* 2, *singularis* 2, *ricordii* 2, *chlorocyanus* 4, *whitemani* 4, *monticola* 2, *cochranae* 1, *crisphei* 2, *etheridgei* 2, *koopmani* 2, *shrevei* 2, *semilineatus* 2, *hendersoni* 2, and *olssoni* 4. The analysis shows that the dentaries of *hendersoni* and *singularis* are relatively more slender than the fossil, the dentary of *chlorocyanus* has the same shape as the fossil, and the dentaries of all other species are relatively less slender. Measurements of the dentary of a modern individual of *A. chlorocyanus* 64 mm snout-vent length are very close to those of the fossil: tooth row length 9.4, depth at the last tooth 1.4, and depth midway between the first and last tooth 1.0 mm. The jaw contains 26 teeth, the fossil contained 28. The fossil is therefore believed to have come from an individual of *Anolis chlorocyanus* about 64 mm snout-vent length. The species occurs over most of the island and probably lives in the immediate vicinity of Cerro de San Francisco today.

Referred Specimen. Dentary 10087.

Leiocephalus Gray

Until recently the genus *Leiocephalus* included a number of South American species as well as those in the West Indies. The continental forms have been shown to be unrelated to the insular species, and *Leiocephalus* has been restricted to the latter (Etheridge, 1965). *Leiocephalus* now occupies the islands of Hispaniola, Navassa, the Caymans, Cuba, and the Bahamas, and a recently extinct form occurred on Martinique. An extinct species has been described from the late Pleistocene of Barbuda and other extinct forms have been reported, but not described, from the Pleistocene of Hispaniola and Jamaica (Etheridge, 1964) and the Miocene of Florida (Estes, 1963). On the basis of osteological characteristics of *Leiocephalus* given in these publications a number of fossils from the cave in Cerro de San Francisco may be referred to the genus. Two species are represented in the fossils, a small one assigned to a modern Hispaniolan species and a very large one that is extinct. In reference to its most obvious diagnostic character, an open Meckelian groove, the extinct species may be known as

Leiocephalus apertosulcus, new species

Holotype. A right dentary, No. 3404 in the vertebrate paleontological collections of the Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

Type Locality. Stratum 2, cave in Cerro de San Francisco, Municipio Pedro Santana, Provincia San Rafael, Republica Dominicana. Probably Late Pleistocene. Collected by Dr. Clayton E. Ray in August or September, 1958.

Referred Specimens. Dentaries 10088-9 (50), maxillae 10090-91 (36), frontals 10092 (6), parietals 10093 (6), jugals 10094 (3), post-orbital 10095, pterygoid 10096, quadrates 10097 (2), articular + surangular 10098, prefrontal 10098, basale 10099, pelves 10100 (15), caudal vertebrae 10101 (6).

Diagnosis. *Leiocephalus apertosulcus* differs from all other species in the genus, both living and extinct, in having Meckel's canal exposed as a deep groove along the lingual face of the dentary; in all other forms it is a tubular cavity completely surrounded by bone. The maximum snout-vent length of this species was at least 150 mm and possibly as great as 200 mm. This exceeds the maximum length attained by any living species (130 mm) and is equaled only by the extinct Barbudan species *Leiocephalus cuneus*.



Fig. 2. Lingual view of the dentary of *Leiocephalus apertosulcus*; type specimen.

Description of Type (Fig. 2). The specimen is 17.2 mm long from its broken posterior border to the symphysis. The tooth row, measured in a straight line from the projected anterior border of the first tooth to the projected posterior border of the last tooth (both are missing) is 16.7 mm long. The height at the position of the penultimate tooth is 4.0 mm. There are 23 teeth or unoccupied alveoli; missing are (front to back) teeth number 1, 2, 4, 18, and 23, and tooth number 13 lacks its entire crown. Teeth

number 3, 5, and 6 are simple, bluntly conical and curve inward and slightly backward. Tooth number 9 and all teeth posterior to it have a tall, slender, straight-sided shaft and a crown that is flared in an anterior-posterior direction, linguo-labially compressed to form a moderately sharp cutting edge, strongly tricuspid and curved inward. The anterior and posterior cusps of each tooth are smaller than the median cusp and separated from it by a wide groove that fades out at the base of the crown. The occlusal edge of each of these teeth is slightly oblique to the main axis of the tooth row. The tricuspid teeth become closely crowded posteriorly, where the anterior cusp of each tooth is overlapped labially by the posterior cusp of the preceding tooth. About 40 per cent of each tooth rises above the alveolar border of the dentary. Teeth number 7, 8, and 9 are transitional in form between the anterior simple teeth and the posterior tricuspid ones. A vertical row of very small foramina penetrate the lingual face of the dentary in the narrow spaces between the teeth.

The labial face of the dentary is smooth and convex. Five large mental foramina form a row on the labial face between the third and tenth tooth; a smaller foramen is present below this row at the position of the eighth tooth. A large, shallow, triangular and slightly concave depression in the posterodorsal part of the labial face extends to the level of the twentieth tooth, marking the former position of the anterolateral process of the coronoid. The lingual face of the dentary is produced medially as a narrow shelf below the base of the tooth row from the symphysis to the nineteenth tooth; beyond this the shelf has been broken away. Meckel's canal is exposed lingually as a wide, open groove that extends the entire length of the dentary.

Referred Specimens: Dentaries. In addition to the type there are 28 nearly complete dentaries and fragments of 22 others. In the complete dentaries the length of the tooth row, measured as in the type, ranges from 9.4-18.2 mm. The number of teeth increases ontogenetically from 17 in the smallest to 25 in the four largest dentaries (Fig. 3). The first two teeth are present in several specimens and, like the third, fifth, and sixth teeth of the type are simply pointed. The first tooth with a distinctly flared and tricuspid crown (number 9 in the type) varies from number 7 to 11. There are 4-7 mental foramina. They occur as far forward as the position of the first tooth and as far posteriorly as the

position of the sixteenth. In dentaries larger than the type the upper half of the labial face becomes flattened to slightly convex posteriorly and develops light surface rugosities. Pathological malformations of bone are present in two of the dentaries. In all other respects the additional dentaries are very similar to the type. Particularly important is the consistent presence of an open Meckelian groove. In one specimen the upper and lower borders of the groove converge and touch for a short distance below the twelfth to fourteenth tooth, but in all others the borders of the groove are widely separated for their entire length.

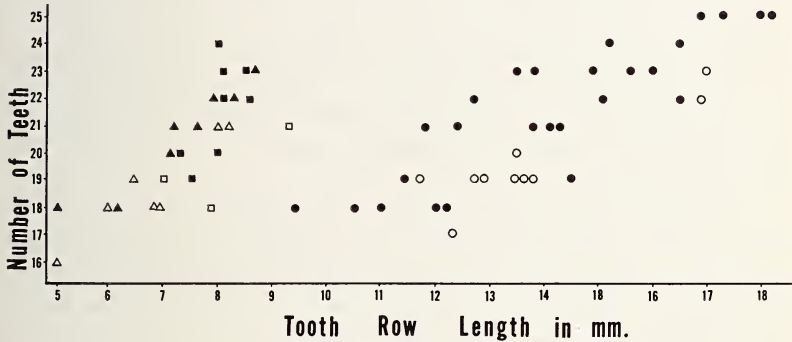


Fig. 3. Ontogenetic increase in the number of teeth on the dentary (solid symbols) and maxilla (open symbols) in two species of *Leiocephalus*. Circles, *L. apertosulcus*. Squares, *L. personatus* from Cerro de San Francisco. Triangles, modern *L. personatus*.

Maxillae. Ten nearly complete maxillae and fragments of 26 others. The length of the tooth row varies from 11.7-17.0 mm. The number of teeth increases ontogenetically from 17-23 (Fig. 3). The crown profiles of the teeth are similar to those of the dentary: simply pointed anteriorly and tricuspid posteriorly. The first tooth with a distinctly flared, tricuspid crown varies from number 5 to 8. The addition of one half of the number of premaxillary teeth (3-4 based on living species) to those of each maxilla places the transition from simple to tricuspid at approximately the same position that it occurs on the dentary. From 6-9 mental foramina form an irregular row above the levels of the second to fourteenth tooth. From 3-5 additional foramina penetrate the ascending nasal process above the row of labial foramina.

Frontals. Six frontal bones lack parts of their nasal processes

but are otherwise nearly complete. The largest measures 4.1 mm across its narrowest interorbital width and 12.3 mm wide along its parietal border. The dorsal surface is concave between the orbits, flattening out toward the nasal-prefrontal and parietal borders. A smooth, shallow, semilunar depression in the upper medial face of each nasal process indicates the former position of the nasal bone and a depression along the ventrolateral face of each nasal process indicate the former position of the prefrontal. These sutural surfaces are not continuous across the upper face of the nasal processes, indicating that the nasals and prefrontals were separated posteriorly above by the anteriorly projecting nasal processes of the frontal. In the middle of the parietal border a deep, U-shaped notch, bordered on each side by a rounded projection, forms the anterior border of the parietal foramen. The entire upper surface of the frontal is moderately rugose; however, the rugosities do not form regularly arranged areas corresponding to the scales that were above them.

Parietals. Six parietals exhibit the ontogenetic change in the shape of the roofing part that is characteristic of all of the larger members of the genus (Etheridge, 1965). The largest measures 13.7 mm wide across its frontal border and 7.3 mm from the frontal border to the occipital crest. The smallest is 9.6 mm wide across its frontal border. The upper surface of the roofing part is moderately rugose in the larger fossils; however, the rugosities do not form regularly arranged areas corresponding to the scales that were above them.

Jugals. The largest of three jugals lacks the distal extremity of its temporal process, but the estimated straight-line distance from the tip of the maxillary process to the tip of the temporal process is 15 mm. One (in two specimens) or two large suborbital foramina penetrate the labial face of the proximal part of the maxillary processes; three smaller foramina penetrate the ventral edge of the temporal process.

Postorbital. A single postorbital is 7.4 mm high from the top of its frontal process to the ventral border. The outer face of the element is strongly sculptured.

Pterygoid. A left pterygoid is 7.4 mm wide between the posteromedial corner of the palatine portion and the lateral extremity of the ectopterygoid process. The anterior end of the palatine process and the posterior end of the quadrate process are missing.

The medial part of the ventral surface of the palatine process is slightly sculptured, but there is no trace of teeth or unoccupied alveoli.

Quadrates. The larger of two quadrates measures 5.8 mm from the top of the cephalic condyle to the bottom of the ventral condyle.

Articular + surangular. A fused articular and surangular is 19.3 mm long; its articular part is 16.1 mm long. The former positions of the angular, coronoid, and dentary are clearly indicated by sutural scars. The angular extended posteriorly below the ventral faces of the articular and surangular almost to the level of the articular condyle. The dentary extended at least as far as the posterior limit of the coronoid. A short, robust angular process projects medially from the articular condyle for a distance of 2.1 mm. Its dorsal surface is smoothly convex, becoming somewhat flattened and turned upward distally. The convex anterior border of the angular process is continuous with the medial border of the articular. The retroarticular process projects posteriorly from the articular condyle for a distance of 3.2 mm. The lateral and medial borders are somewhat raised. The angular and retroarticular processes are united posteromedially by a thin shelf whose margin forms a nearly straight line between the distal extremities of the two processes.

Prefrontal. A single prefrontal is 8.7 mm long from the anterior tip of the maxillary process to the posterior tip of the frontal process. Its outer surfaces are distinctly rugose.

Basale. A basale, consisting of a basisphenoid, two otic elements, and the occipital bones, is apparently from a subadult individual. The bones were held together by cave earth that filled the brain cavity, but they fell apart when the matrix was removed. The distance between the extremities of the basicranial tubercles is 5.0 mm.

Pelves. Fifteen pelves are apparently from adult individuals, for in all of them the ischium, ilium, and pubis are firmly ankylosed. Measurements of a complete specimen are: greatest length from the anterior end of the pubis to the posterior end of the ilium 24.7, greatest height from the ventral border of the ischium to the upper border of the posterior prominence of the ilium 13.4, greatest diameter of the acetabulum 5.0 mm. The acetabular diameter of the smallest specimen is 4.3, of the largest 6.4 mm.

Caudal Vertebrae. Three anterior segments and three posterior segments of autotomic caudal vertebrae are referred to this species. The diameter of the neural arch just anterior to the condyle of the posterior segments ranges from 1.7-2.2 mm. Eight smaller posterior segments may be from subadults or from a more posterior part of the tail of this species, or they may have come from individuals of the smaller species of *Leiocephalus* in the cave. In all of the posterior segments a thin, median crest extends along the top of the neural arch from the neural spine to the fracture plane, where it rises to form the posterior part of what was probably a narrow, triangular spine above the fracture plane prior to dissociation of the two segments. The anterior border of the posterior segment (the posterior border of the fracture plane) is more or less vertical except for a notch on each side near the bases of the neural arch, the notch marking the former position of the base of the transverse process of the anterior segment.

The anterior segments of the autotomic caudal vertebrae also possess a thin, median crest that rises steeply as it approaches the fracture plane. Their transverse processes are spatulate, slightly tapered and oriented more or less laterally.

Comparisons. The presence of an open Meckelian groove in the dentary of *Leiocephalus apertosulcus* is unique within the genus. In all other forms, both living and extinct, Meckel's canal is a tubular cavity completely surrounded by bone. Among the iguanid genera allied to *Leiocephalus* (*Tropidurus*, *Liolaemus*, *Stenocercus*, *Proctotretus*, *Platynotus*, *Plica*, *Ophryoessoides*, *Uranoscodon*, and *Urocentron*) an open Meckelian groove occurs only in some species of *Liolaemus* (Etheridge, 1965). *Leiocephalus* and *Liolaemus* show many similarities; present in both but absent in all other genera listed above are a large descending process of the coronoid that laterally overlaps the dentary, evident by the coronoid scar on the fossil dentaries, and a lamination of the nasal spine of the premaxilla by the nasal bones. On the basis of these and other similarities of the skeleton and integument I suggested that, of the genera listed above, *Liolaemus* is probably most closely allied to *Leiocephalus* (Etheridge, 1965). There are, however, numerous osteological differences between the two, some of which are evident in the fossils and permit their certain identification as *Leiocephalus*: the presence of vertical rows of small foramina in the lingual face of the jaws in the narrow spaces between the teeth,

the strongly converging lateral borders of the adult parietal, and the presence of a vertical spine-like process above the plane of fracture of the autotomic caudal vertebrae. Although the Hispaniolan fossils are clearly referable to the genus *Leiocephalus*, the presence of an open Meckelian canal in this extinct species provides additional evidence for the close relationship of *Leiocephalus* with *Liolaemus*.

The snout-vent lengths of the animals from which the fossils came have been calculated by multiplying various measurements of the same elements of living species to their snout-vent lengths. Assuming the proportions that existed in the extinct species fall within the limits of those which exist among all of the living forms, a minimum and maximum estimate of snout-vent length may be obtained for the extinct species. The minimum and maximum estimates for the largest fossil of each of several elements are as follows: dentary 142-173 mm, maxilla 144-178 mm, parietal 141-178 mm, frontal 139-161 mm, postorbital 133-185 mm, articular + surangular 147-192 mm, and pelvis 161-202 mm. The maximum snout-vent length attained by any living species is 130 mm recorded for *Leiocephalus carinatus microcyon* (Schwartz, 1959). The largest living Hispaniolan species is *L. melanochloris*, which attains a maximum snout-vent length of 108 mm (Cochran, 1941). All of the minimum values calculated for *Leiocephalus apertosulcus* exceed 130 mm; thus, the species probably attained a greater size than any living species of the genus, and certainly must have grown larger than any living Hispaniolan form. On the basis of the same type of calculations the maximum snout-vent length attained by the extinct Barbudan species, *L. cuneus*, was also estimated to have been nearly 200 mm (Etheridge, 1964).

Leiocephalus personatus Cope 1862

The smaller of the two species of *Leiocephalus* from the cave in Cerro de San Francisco appears to be referable to the extant Hispaniolan species, *L. personatus*. This species and *L. pratensis* differ from all other forms of *Leiocephalus* in that the upper surfaces of the frontal and parietal bones are distinctly sculptured after the pattern of scales that were above them. Impressions of the posterior parts of the interparietal and the inner parietals and of the medial parts of the outer parietal scales are present on the

roof of the parietal bone, and impressions of the anterior parts of the interparietal and inner parietals and of the frontoparietals and posterior frontal scales are present on the roof of the frontal bone. These scale impressions are clearly evident on the fossil parietals and frontals of the smaller species. The skull of *Leiocephalus pratensis* differs from that of *L. personatus* in that the interorbital width of the frontal bone is relatively greater: the ratio of the posterior width of the frontal to the narrowest interorbital width is about 2.3 in *pratensis* and about 3.3 in *personatus*. This ratio is 3.5 in the fossil frontals.

Fossil maxillae and dentaries referred to *L. personatus* lack the open Meckelian groove of *L. apertosulcus*, excluding the possibility that these small jaws are from subadult individuals of the latter. Furthermore, a plot of the maxillary and dentary tooth row lengths against the number of teeth indicates that different gradients in the ontogenetic increase in tooth numbers exist between the two species (Fig. 3). In this and in all other respects the fossil maxillae and dentaries are indistinguishable from those of Recent *L. personatus*.

Measurements of the largest fossils are as follows: dentary tooth row 8.6, maxillary tooth row 7.9, anterior width of parietal roof 7.1, posterior width of frontal 4.8 mm. Using measurements of Recent skeletons of *L. personatus* as a basis, the snout-vent lengths calculated for the largest fossils are: based on dentary 75 mm, on maxilla 74 mm, on parietal 73 mm, on frontal 67 mm. These estimates are within the range of maximum snout-vent lengths of the various living races of the species: 55 mm in *L. p. louisae* to 83 mm in *L. p. mentalis* (Cochran, 1941).

Leiocephalus personatus occurs throughout the island today.

Referred Specimens. Dentaries 10102 (10), maxillae 10103 (3), frontals 10104 (2), parietals 10105 (4).

TEIIDAE

Ameiva chrysoleama Cope 1869

Several cranial elements, pelves, and vertebrae are referred to *Ameiva chrysoleama* because of their large size and close structural resemblance to modern skeletons of the species. The jaws of *A. chrysoleama* differ from those of *A. taeniura* and *A. lineolata* by the possession of no more than 4 tricuspid teeth on the rear of

the maxilla and no more than 5 tricuspid teeth on the rear of the dentary. *A. taeniura* and *A. lineolata* have from 6-11 tricuspid teeth on the rear of the maxilla and from 7-13 on the rear of the dentary. The fossil jaws assigned to this species have from 0-3 tricuspid teeth.

Ameiva chrysolaeama reaches a maximum snout-vent length of 160 mm, *A. lineolata* a maximum of 56 mm, and *A. taeniura* a maximum of 80 mm (Schwartz, *in litt.*). Snout-vent lengths of the smallest and largest fossils referred to *A. chrysolaeama* are: based on dentaries 97-125 mm, on maxillae 105-114 mm, on frontals 104-128 mm, on quadrate 134 mm, and on pelves 90-125 mm. Thus even the smallest fossil exceeds *A. taeniura* and *A. lineolata* in size.

Three ameivas occur on Hispaniola today. *A. chrysolaeama* and *A. taeniura* are widely distributed and probably occur in the immediate vicinity of Cerro de San Francisco. *A. lineolata* is restricted to certain limited areas and probably does not live near the cave today. Two other species are confined to off-shore islands: *A. barboursi* to Goanve Island and *A. rosamonde* to Saona Island.

Referred Specimens. Dentaries 10106 (9), maxillae 10107 (2), frontals 10108 (2), quadrate 10109 (1), pelves 10110 (4), vertebrae 10111 (6).

Ameiva taeniura Cope 1862

Several jaws and a pelvis are referred to *Ameiva taeniura* because of their moderate size and possession of at least 7 tricuspid teeth on the rear of the jaws. Although I am unable to distinguish structurally the modern skeletons of *A. taeniura* and *A. lineolata* the fossils are too large to be assigned to *A. lineolata*. Snout-vent length estimates for the fossils are: based on dentaries 76-81 mm, on maxillae 70-76 mm, on pelvis 72 mm.

Referred Specimens. Dentaries 10112 (3), maxillae 10113 (3), pelvis 10114 (1).

ANGUIDAE

Diploglossus sternurus Cope 1862

About 100 fossils are referred to *Diploglossus sternurus* entirely on the basis of their large size. The six diploglossine lizards known to occur on Hispaniola today, *Diploglossus curtissi*, *D. costatus*, *D. sternurus*, *D. darlingtoni*, *Wetmorina haetiana* and *Saurisia sep-*

soides, are very similar osteologically; they differ primarily in skull and girdle proportions and in maximum size attained. The maximum snout-vent length in these forms is as follows: *D. sternurus* 230 mm, *D. costatus* 127 mm, *D. curtissi* 86 mm, *D. darlingtoni* 67 mm, *W. haetiana* 87 mm, and *S. sepsoides* 46 mm (Cochran, 1941; Schwartz, unpublished manuscript). The fossil basale and pelves in which the components are completely ankylosed indicate that two size classes of *Diploglossus* are present, one with a maximum snout-vent length of 120-130 mm and one with a maximum length of 210-250 mm. These figures are close to the maximum sizes of *D. costatus* and *D. sternurus* today. For this reason all fossils estimated to have come from animals over 130 mm snout-vent length are referred to *Diploglossus sternurus*. This species occurs widely over the island and probably lives in the immediate vicinity of the cave today.

Referred Specimens. Dentaries 10115 (38), maxillae 10116 (22), premaxillae 10117 (4), parietals 10118 (4), articulares 10119 (5), pterygoids 10120 (4), basale 10121 (1), pelves 10122 (3), sacral vertebrae 10123 (5), caudal vertebrae 10124-5 (11).

Diploglossus costatus Cope 1861

The fossil pelves and basale from adult individuals calculated to have been 120-130 mm snout-vent length are referred to this species. About 100 other fossils of *Diploglossus* are estimated to have come from animals less than 130 mm snout-vent length. There is no way to determine whether fossils of this size are from *D. costatus* or from subadult *D. sternurus*. Both species are probably represented in these smaller fossils. *Diploglossus costatus* also occurs widely over the island and probably in the immediate vicinity of the cave today. The ranges of the other Hispaniolan diploglossines do not now include Cerro de San Francisco.

Referred Specimens. Pelves 10126 (3), basale 10127 (2). Referred to *Diploglossus* sp.: dentaries 10128 (34), maxillae 10129 (31), articulares 10130 (4), pterygoids 10131 (2), sacral vertebrae 10132 (4), caudal vertebrae 10133-4 (25).

ABSENCE OF ANOLIS DISTICHUS

Anolis distichus is widespread on Hispaniola and has been taken in the immediate vicinity of Cerro de San Francisco. If it

had lived there at the time the cave deposits were formed it might reasonably be expected among the fossils. The argument for this concerns the manner in which the deposits were formed. Nearly all of the fossiliferous West Indian caves contain abundant chiropteran remains. Most of the other vertebrate fossils appear to have originated from owl pellets (Miller, 1929; Anthony, 1919; Hecht, 1951). This is almost certainly the origin of the lizard fossils in the cave at Cerro de San Francisco. The remains of a barn owl, *Tyto alba*, a burrowing owl, *Speotyto cunicularia*, and one or two other owls, probably of the genus *Asio*, have been identified from this cave (Brodkorb, *in litt.*). The extinct, giant barn owl, *Tyto ostologa*, described from a cave in Haiti (Wetmore, 1922) is absent. Hecht (1951) reported the predation by barn owls on *Anolis*, *Diploglossus* and *Aristelliger* in Jamaica. Wetmore and Swales (1931) reported the remains of *Anolis ricordii* and *Ameiva* sp. in modern pellets of *Tyto alba* on Hispaniola. I have examined modern owl pellets from near the mouth of a cave near Boca de Yuma, Province Altagracia, Dominican Republic, collected by Clayton Ray. They contain a large number of bones of *Anolis ricordii*, *A. chlorocyanus*, *A. distichus*, and *A. cybotes*. A single intact pellet contained bones of at least 16 individuals of *Anolis*.

Barn owls rarely hunt before dark. Arboreal, nocturnal lizards, such as *Aristelliger*, and lizards that sleep in exposed places, such as *Anolis*, are to be expected in their pellets. It is difficult to imagine what sort of opportunity they might have to prey on strictly diurnal lizards that sleep in concealed places, such as *Leiocephalus* or *Ameiva*. The more diurnal, burrowing owls may be the chief predators of the latter. As one might expect, fossorial lizards (*Amphisbaena*) and very small lizards (*Sphaerodactylus*) do not occur in the cave deposits.

Except for *Leiocephalus apertosulcus*, which is extinct, all of the lizards identified among the Cerro de San Francisco fossils probably occur in the immediate vicinity of the cave today. Other lizards that probably occur there now are *Amphisbaena manni*, *Sphaerodactylus* sp., *Anolis olssoni* and *A. distichus*. *Amphisbaena* and *Sphaerodactylus* have not been found in any West Indian cave deposits and are not to be expected here. *Anolis olssoni*, because of its small size and habitat of low bushes and grass is probably also not to be expected. In the owl pellets from Boca de Yuma the only local anole not present in the pellets is *Anolis semilineatus*,

a species with similar habits and of similar size to *A. olssoni*. Thus, the only lizard that occurs at Cerro de San Francisco today but not in the cave, whose presence among the fossils may be reasonably expected if it had lived there, is *Anolis distichus*. The minimum size of fossil *Anolis* in the cave is 35 mm snout-vent length, well below the maximum size of 50 mm of *A. distichus*. That this species is subject to owl predation is verified by its presence in large numbers in the modern pellets from Boca de Yuma. It is difficult to account for the absence of *Anolis distichus* in more than 2000 lizard fossils except by the assumption that it actually did not occur there when the deposits were formed.

SUMMARY

Many thousands of vertebrate fossils were recovered from a cave in Cerro de San Francisco in the western part of Dominican Republic. Most of the non-chiropteran remains are probably from owl pellets. Among the fossils are eleven species of lizards, one of which is extinct; the others probably occur in the vicinity of the cave today.

Bones of a large gekko, *Aristelliger lar*, are from individuals between 57-140 mm snout-vent length. The largest slightly exceed the maximum size of the species today.

A large anole, *Anolis ricordii*, is represented by bones from individuals between 78-192 mm snout-vent length. The largest exceed by 30 mm the maximum size of the species today. Fossils of *Anolis cybotes* are from individuals between 42-75 mm snout-vent length, and a single bone of *Anolis chlorocyanus* is from an individual 64 mm snout-vent length. Both species attained approximately the same maximum size as they do today.

Two anoles, *Anolis olssoni* and *Anolis distichus*, that occur near the cave today were not identified among the fossils. The absence of *Anolis distichus* probably indicates that it did not actually live there at the time the cave deposits were formed.

Two species of *Leiocephalus* were recovered from the cave. One of them, *L. apertosulcus*, is extinct. It is not closely related to any living form and differs from all of them in possessing an open Meckelian groove. It is calculated to have reached a maximum snout-vent length of about 200 mm, larger than any living member of the genus and equaled in size only by the extinct Bar-

budan species *L. cuneus*. The smaller species is referred to *Leiocephalus personatus*. It reached a maximum snout-vent length of about 75 mm, within the range of maximum sizes attained by the various races of that species today.

Two ameivas are identified, *Ameiva chrysoleama* from individuals between 90-134 mm snout-vent length and *Ameiva taeniura* from individuals between 70-81 mm snout-vent length. Neither species exceeded the maximum size attained by individuals today.

Two galliwaspes, *Diploglossus sternurus* and *D. costatus*, are present among the fossils. The largest specimens of *D. sternurus* are from individuals 210-250 mm snout-vent length, and the largest specimens of *D. costatus* from individuals 120-130 mm snout-vent length, approximately the same maximum size reached by these species today.

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